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19. ABSTRACT (Continue on reverse if necessary and identify by block number)

Four research goals were accomplished. 1) It was determined that sensory responsiveness of primary somatosensory (SI) cortical neurons to vibratory stimuli is quantitatively different depending upon whether monkeys make wrist movements in response these stimuli or withhold movement. 2) For a special class of SI neurons, it was determined that activity occurring before movement is comprised of a reactivation of the neuron's sensory response and a presumably centrally generated component. 3) It was determined that sensory responsiveness and premovement activity are elevated when behavioral conditions are unpredictable as compared to when they are predictable. 4) It was determined that human subjects can acquire a positional target by wrist movements more quickly if vibratory go-cues are presented in addition to the illumination of a visual signal lamp. The neurophysiological experiments suggest that the responsiveness of SI neurons is profoundly affected by behavioral conditions and an animal's expectation of correct performance. The human psychophysical experiments suggest that the addition of vibratory go-cues to control systems may have benefits without seeming to degrade performance.

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Research Objectives

Four research goals were accomplished during this second year of USAF grant AFOSR 88-0179. (1) It was determined that sensory responsiveness of primary somatosensory (SI) cortical neurons to vibratory stimuli is quantitatively different depending upon whether monkeys make wrist movements in response to these stimuli or withhold movement. (2) For a special class of SI neurons, it was determined that activity occurring before movement is comprised of a reactivation of the neuron's sensory response and a presumably centrally generated component. (3) It was determined that sensory responsiveness and premovement activity are elevated when behavioral conditions are unpredictable as compared to when they are predictable. (4) It was determined that human subjects can acquire a positional target by wrist movements more quickly if vibratory go-cues are presented in addition to the illumination of a visual signal lamp. The neurophysiological experiments suggest that the responsiveness of SI neurons is profoundly affected by behavioral conditions and an animal's expectation of correct performance. The human psychophysical experiments suggest that the addition of vibratory go-cues to control systems may have benefits without seeming to degrade performance.

Status of Current Research - Statement of Work

Each of the four conducted studies used a behavioral paradigm that had many features in common. The basic paradigm will be described and then the variations used in the individual studies.

Basic Behavioral Paradigm - Monkeys

Five adult male rhesus monkeys (*Macaca mulatta*) , 8.0 - 10.9 kg, were trained to make flexion and extension wrist movements in response to vibratory cues. Three of the five also were trained to make these movements in response to visual stimuli. All were cared for in accordance with the *NIH Guide for Care and Use of Laboratory Animals, revised 1985*. Each monkey sat in a specially designed chair in a quiet, moderately lit (5 foot-candles) room and viewed a visual display placed 35 cm directly in front of them at eye level. This display contained 31 light-emitting diodes (LED) located behind a semiopaque grey acrylic plate. The display consisted of a large, red LED centrally located between vertical rows of smaller, yellow LEDs. The display was coupled to the output of a wrist position transducer. Each successively illuminated LED above or below the central LED corresponded to an angular deflection of 1° from the central position. The monkey's hand rested on a flat aluminum handle coupled at one end to the axle of a brushless DC torque motor. His forearm was supported by an arm rest.

Each trial was initiated when the monkey centered the handle, thereby illuminating the central LED. The handle had a load which provided a constant torque of 0.07 Nm in the direction of extension. At the start of each trial, a combination of two instruction LEDs was sometimes presented. The LEDs were located in the upper left corner of the visual display (11.8° of visual angle from the center). The presence or absence of illumination of each LED instructed the monkey about the direction of the required movement (a red LED on meant extension and off meant flexion) and the type of sensory stimulus that would be presented in that trial (a green LED on meant visual and off meant vibratory). These LEDs also warned the monkey that a trial had started. The monkey maintained a centered wrist position for 0.5, 1.0, 1.5 or 2.0 s. The hold time for each trial was obtained from a computer

algorithm, running in real-time, that produced a uniform distribution of the four periods. Autocorrelation analysis indicated that there was no statistically significant sequential structure to the output of this pseudo-random number generating algorithm. If the monkey maintained a steady position within ±0.5° (each lamp =1°) of center, a vibratory or visual stimulus was presented and the current wrist position was designated as the start position for analysis. Vibratory cues consisted of vibrating the handle by driving the motor with a low-amplitude sine wave (<0.057° or less than 100 μm peak-to-peak measured 10 cm distal to the coupling of the handle to the motor) at either 27, 57, or 127 Hz. Visual cues consisted of adding or subtracting a DC voltage from the wrist position signal, resulting in a shift in the illuminated lamp (±2.4° of visual angle from display center) in the opposite direction from the requested movement by an amount equal to that required to recenter the display (5.0°). Sensory stimuli remained on until the monkey moved at least 5° from the start position. It was determined that the first change in handle position 0.1° from the start position following stimulus onset gave the most reliable indicator of the actual start of the movements. This was designated as the first detectable change in position. Its occurrence after stimulus onset was entered into the data stream. The ballistic movements made by the monkeys were not restricted in speed and amplitude other than by stops in the apparatus at ±30° of angular deflection from center. Flexion and extension movements were requested in alternating blocks of 10 trials each. When both vibratory and visual stimuli were used, they were pseudo-randomly distributed within blocks for a given vibratory stimulus frequency. Randomization was accomplished with the same computer algorithm described above. Monkeys received an audible "click" and fruit juice reward if the movement was made in the appropriate direction. This click informed the monkey that the trial was successful. It also served as a signal for the monkey to recenter the handle to begin the next trial.

The Sensory Responsiveness Paradigm - Monkeys

Three monkeys performed two sensory responsiveness tasks. During the "movement task" they made wrist flexion or extension in response to vibratory stimuli only. In the "no-movement task" they withheld movement following the presentation of only the vibratory stimuli. The display was turned off at the start of the first trial during the no-movement task to indicate which task the animal should perform. Trials for each task began in the same manner, with the monkey centering the plate. If the monkey maintained this centered position during the hold period, the plate was vibrated (as described above). Movement of more than 0.5° from center during the hold period cancelled the trial.

At this point, the two tasks differed. In the movement task, the vibratory stimulus, which served as the go-cue, remained on until the monkey either flexed or extended at least 5° from the held position. If he made the requested movement, the monkey received a fruit juice reward. In the no-movement task, the vibratory stimulus remained on for 1 s. If the monkey held the centered position within 0.5° for this 1 s period, he was rewarded. Otherwise, the trial was cancelled. In both tasks, a new trial was begun when the monkey once again held a steady position.

The Multimodal Paradigm - Monkeys

Three of the five monkeys ran this paradigm and were first trained to perform wrist flexion and extension movements in response to vibratory cues only. Once animals reached a stable level of performance,they were trained to make wrist movements in response to visual cues as well. After an initial period during which these animals learned to make the appropriate movements in response to either type of cueing stimulus, their performance again stabilized.

The "Unexpected Failure" Paradigm - Monkeys

One monkey was trained to perform the standard vibratory-cued wrist flexion and extension paradigm, with one variation. In this instance, correct performance of the task was rewarded only 75% of the time. In the other 25% of the correctly performed trials (pseudo-randomized within blocks), the reward for correct performance was withheld.

The Target Reaction Time (RT) Paradigm - Human Subjects

Nine human subjects made 5° reaction time wrist flexion or extension movements to visual target. Subjects were seated in a comfortable chair and performed these movements with their preferred hand. The visual display that they viewed was the same as that described above and was placed 50cm directly in front of them at eye level. Hold period and vibratory stimulation parameters were as described above. However, these subjects held the centered handle position against a 0.12 Nm load which assisted extension movements.

Following a hold period of 0.5, 0.75, 1.0 or 1.5 s (pseudo-randomized), a target was illuminated. This target was one of the LEDs of the visual display used to indicate current wrist position. The subject's task was to make a wrist movement to align the cursor LED with the target and hold it there. This required a 5° wrist flexion or extension movement. Two types of movement cues ("go-cues") were used. The first was the illumination of the target alone. The second was the illumination of the target *and* a vibration of the handle at 27, 57 or 127Hz. If they maintained alignment for 0.5 s, a "click" indicated that the trial had been performed correctly. A new trial was begun once the subjects recentered the handle. Flexion and extension movements were alternately made in blocks of 10 trials. Target alone or target plus vibration cues were pseudo-randomly presented within each block of trials.

Electrophysiological Recording and Histology - Monkeys

Once the animals had reached a level of steady behavioral performance, they were prepared for single-unit electrophysiological recording. The details of this preparation, the daily maintenance of the animals, and the preparation of histological sections following the experiments have been presented elsewhere (Nelson 1988). Briefly, a stainless steel chronic recording chamber and head restraint devices were surgically implanted. Transdural penetrations were made daily into the cortex using platinum-iridium microelectrodes. Neuronal activity was amplified, filtered and discriminated by conventional means. Analog signals corresponding to the animal's current wrist position were sampled at 100 Hz. These signals, as well as data related to the timing of behavioral events and neuronal activity, were collected and stored in a microcomputer. When possible, a group of at least 80 trials was collected for each movement at a given vibratory stimulus frequency whether or not visual cues were also used. After recording the activity of each neuron, the animal was examined for the location and type of the neuron's receptive field (RF) by lightly touching skin surfaces, manipulating joints, and kneading muscles. Each animal had been previously trained to remain quiescent during RF testing. The RFs were classified as "cutaneous" if the neurons preferentially responded to light touch and "deep" if they responded to bending of a single joint or palpation of the belly of a muscle that moved the fingers or wrist. In one monkey, the recording sites were micro-stimulated (train of 11 cathodal pulses; 200 μs pulse duration at 330 Hz).

Following the last recording day, the animals were deeply anesthetized with sodium pento-barbital and transcardially perfused with 10% buffered formol-saline. Histological sections of the cortex were prepared and the electrode tracks were reconstructed (Nelson and Douglas 1989).

Data Analysis

Data analysis for the monkey electrophysiological experiments was conducted in several stages. Graphic and numerical displays of the neuronal activity and wrist position were reconstructed by an off-line data analysis routine. Perievent histograms, raster displays of the neuronal activity, and analog displays of the animal's behavioral performance were also examined. These displays were oriented in time either with the onset of the sensory stimulus or with the onset of the sensory-trigger movements. The level of background activity for each set of trials was determined by finding the mean discharge rate during the hold period (measured in spikes/s) and comparing this to the mean discharge rate of neuronal activity during all subsequent phases of the task that preceded movement. Neuronal activity associated with the onset of vibratory stimuli was measured by determining the first monotonic change in activity after stimulus onset in which the magnitude of the change was at least ±40% of the background activity for at least 30 consecutive milliseconds. Premovement activity was measured from displays centered on movement onset using the same temporal and magnitude criteria. Premovement activity was considered to be the first change in activity following the vibratory response or the first activity change following stimulus onset in non-stimulus related neurons and continuing until movement onset. Stimulus-related and premovement activity changes were compared by subtracting the background activity from each.

In the human psychophysical experiments, the time from go-cue stimulus onset until the beginning of movement was measured, yielding RTs. The time from the beginning of movement until the subject's position matched the trigger position was also measured (movement time - MT). Daily average RTs and MTs were calculated for each subject for the 14 days of training. RTs and MTs were separated by movement direction (flexion or extension) and go-cue type (visual only or visual plus vibratory).

1) <u>The Sensory Responsiveness Experiments</u>

These experiments were designed to test the hypothesis that primary somatosensory cortical neurons are more responsive to sensory stimuli when the detection of these stimuli is important for correct behavioral performance and reward as compared with when the same stimuli only predict the reward and do not require that current behavior must be modified.

Summary of Findings

Vibratory stimulus-related responses were recorded from monkey primary somatosensory cortical (SI) neurons while animals performed two tasks. In the movement task, vibratory stimuli served as the go-cue for wrist flexion or extension. In the no-movement task, movements normally made in response to vibratory stimuli were extinguished. Area 3a, 3b, and 1 neurons with deep receptive fields (RFs) exhibited greater stimulus-related activity during the movement task than during the no-movement task. Area 3b neurons with cutaneous RFs were similarly enhanced during the movement task, whereas area 1 neurons with cutaneous RFs were less responsive to vibratory stimuli during the movement task. These results suggest that motor-set and/or selective attention may modulate the responsiveness of SI neurons to peripheral stimuli and that changes in sensory responsiveness in SI neurons differ as a function of their cortical location and RF type.

Results

This study dealt with 6 area 3a, 13 area 3b and 22 area 1 neurons that had vibratory related responses in both tasks, and that had peripheral RFs related to the hand or wrist. Neurons with cutaneous and deep RFs were treated separately. All neurons in the area 3a population had deep RFs. In addition, since the stimulus-related response of a given neuron was often different as a function of the frequency of vibratory stimulation and since the vibratory responses of most neurons were sampled using more than one stimulus frequency, each sample was treated separately. However, no neuron's recordings contributed more than 6 samples to any data group.

Figure 1 illustrates the activity of an SI neurons that exhibited vibratory-related responses during movement and no-movement trials. Shown also are the neuron's receptive field (RF; Figure 1C) and the location of the recording in a drawing of a sagittal section through SI cortex (Figure 1D). This examples illustrates one of the major findings of this study. Neurons in area 1 with cutaneous RFs were less responsive to vibratory stimuli during movement as compared with no-movement trials. In contrast, area 3b neurons with cutaneous RFs were more responsive during movement trials. Neurons with deep RF had enhanced sensory response in movement as compared to no-movement trials.

Activity Difference Measurements

An enhancement index was calculated for each sample by dividing the magnitude of the stimulus-related activity exhibited during movement trials by that observed during no-movement trials. The samples were grouped according to cortical location of the recorded neurons and RF type. The distributions of RF locations for the data groups are listed in Table 1. Using movement direction as a grouping variable, either alone or in combination with cortical location and RF type, did not significantly alter the results presented below. Enhancement indices greater than 1.0 indicate that a neuron was more responsive to a vibratory stimulus when it served as the cue for movement as compared to when it did not. Conversely, enhancement indices less than 1.0 indicate that the opposite was true. Figure 1E shows the distributions of enhancement indices for the samples, grouped by cortical area and RF type. The mean enhancement index for area 1 cutaneous RF neurons was significantly different from the other four groups (one factor ANOVA; $p< 0.01$). This group had only one member for which the enhancement index was greater than 1.0. The mean enhancement indices for the remaining four groups were not significantly different from one another (one factor ANOVA; $p> 0.05$). These groups had enhancement indices distributed over larger ranges. Each of the four remaining groups had mean enhancement indices that were significantly greater than 1.0 (Table 1).

Using a paired *t*-test, the absolute value of the magnitudes of the stimulus-related activity during movement and no-movement trials were compared, grouping the samples by the same variables listed above. Area 1 neurons with cutaneous RFs had significantly smaller vibratory activities during the movement task when compared with the no-movement task (mean difference: -17.49; T=5.49; DF=25; $p<.001$). The vibratory responses of area 3b neurons with cutaneous RF were enhanced during movement trials (mean difference: 7.76; T=3.31; DF=38; $p=.002$). The vibratory activities were larger during the movement as compared with no-movement trials for deep RF neurons located in all three cortical areas. However, only the area 1 deep RF group had a mean difference in responsiveness between the two tasks that was statistically significant (Table 1).

As an additional comparison, the difference in vibratory stimulus-related activity was divided by the absolute value of the larger of the two activities (movement or no-movement trial vibratory responsiveness). This gives a crude measure of the percentage change in responsiveness between the

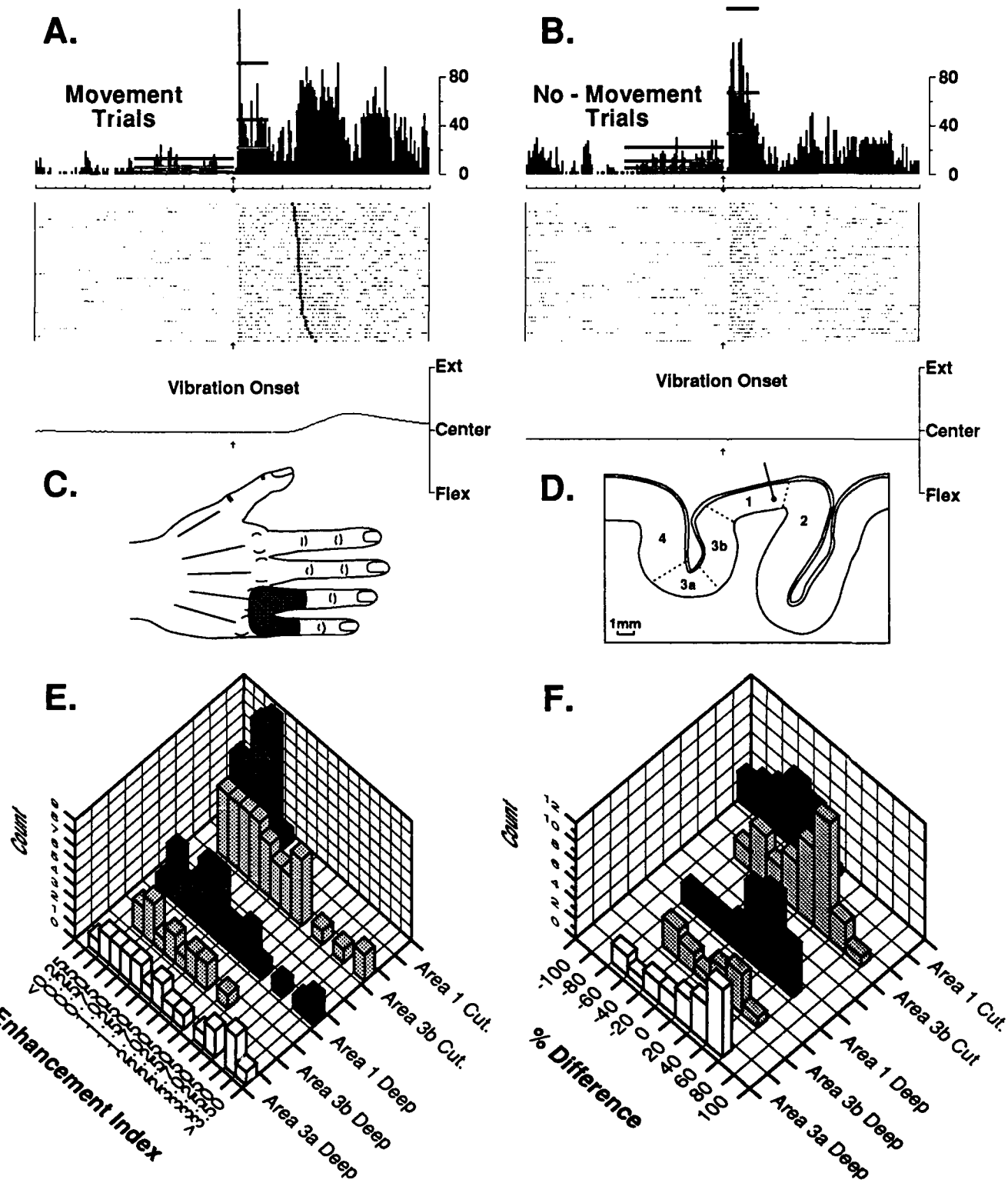


Figure 1. The firing patterns of an area 1 neuron recorded during movement trials (A) and during no-movement trials (B). Panels consist of 3 displays: above, a peri-stimulus histogram; middle, a raster display where each dot represents a single spike and each row and individual trial, and below, the average positional displacement of all trials. Displays are centered on vibratory stimulus onset (57 Hz, A and B). Major ticks below the histograms indicate 250 ms. Open bars in the histograms indicate the duration of measurement of the background activity (left of arrows) and the stimulus response (right of arrows). Middle bars show the mean activity (spikes/s) for the period. Upper and lower bars show the thresholds above or below the mean activity used to determine when a significant activity change occurred. Dark marks in rasters indicate movement onset. Trials in these panels are arranged by increasing reaction time. Full scale deflections from center in either direction on the position traces are 12.5°. (C) The receptive field of the neuron located on the dorsal surface of the hand. (D) Drawing of a sagittal section through SI containing the recording site for this neuron. The distribution of enhancement indices (E) and the percentage differences in vibratory stimulus-related activity (F) between the movement and no-movement conditions for each neuronal recording, grouped by cortical location and receptive field type.

Table 1: Measurements

RF Type	Samples			Enhancement Index		Activity Difference		Percentage Change	
				Mean	SD	Mean	SD	Mean	SD
Deep RFs	Location								
	Flex	Ext	Total						
Area 3a			21	2.01[c]	1.18	6.30	14.25	30.2[b]	42.7
Digits:	2	0							
Wrist:	2	17							
Area 3b			14	1.42[a]	0.59	5.19	23.40	18.9[a]	32.0
Digits:	0	6							
Wrist:	0	8							
Area 1			32	1.75[c]	0.94	5.54[b]	10.11	27.6[c]	37.7
Digits:	4	17							
Wrist:	4	7							
Cut. RFs	Location								
	Ventral	Dorsal	Total						
Area 3b			39	1.72[c]	1.08	7.76[b]	14.65	24.7[c]	35.6
Digits:	3	18							
Hand:	12	2							
Wrist:	0	4							
Area 1			26	0.62[c]	0.29	-17.49[c]	16.23	-38.4[c]	29.6
Digits:	8	2							
Hand:	6	6							
Wrist:	4	0							

Table 1. The distribution of RFs locations by data group and means and standard deviations of the three comparisons of the stimulus-related activity during movement as compared with no-movement trials, grouped by cortical location and RF type. Enhancement Indices and percentage changes were compared using a one factor ANOVA; the differences were compared using a paired *t*-test. The enhancement indices were tested for significance against the hypothesis that they were equal to 1.0; the differences and percentage changes were tested against the hypothesis that they were equal to 0.0. SD = standard deviation
[a]: $p < .05$; [b]: $p < .01$, [c]: $p < .001$.

two task conditions. This was done in an attempt to standardize the difference in activity for each neuron with respect to its vibratory activity firing rate and thus reduce the greater influence that neurons with higher firing rates have on the difference calculations. The mean percentage changes of the five groups are listed in Table 1 and the distributions of these changes by group are shown in Figure 1F. Each mean percentage change was significantly different from 0.0 and paralleled the enhancement indices for the groups. On the average, area 1 neurons with cutaneous RFs were approximately 38% less responsive to vibratory stimuli when these signals were the go-cues for wrist movements. Neurons in the other four groups were more responsive to vibratory stimuli during the movement as compared with the no-movement task. The mean percentage change for the area 1 cutaneous RF neurons was significantly different from all other groups (one factor ANOVA; $p < .001$). These other groups, however, were not different from one another (one factor ANOVA; $p > 0.05$).

Conclusions

The changes in sensory responsiveness observed in this study may result from changes in motor-set or selective attention. This and other studies have shown that the same somatic stimulus may result in different neuronal activity depending upon the type of behavioral response that an animal has been taught to make after detecting stimulus onset. One factor that appears to differ in the two tasks is that in the movement task, the monkeys are prepared to make a movement in response to the vibration and thus may be in a different motor-set than in the no-movement condition. Others have suggested that when vibration is a cue for movement it is a relevant stimulus, whereas vibratory stimuli are presented during no-movement they are irrelevant to the animal's behavior. This, then, would imply that there may be differences in a form of selective attention between the two tasks used in this study.

The present results suggest that changes in sensory responsiveness are somewhat specific rather than general, as might be predicted if they were due to changes in arousal or vigilance. Both enhancement and suppression of stimulus-related activity have been observed. The direction of the relative change for a given group of neurons appears to be related to their cortical location and RF type.

The role of the observed changes in sensory responsiveness is not currently known. One possibility is that cutaneous RF neurons which do not signal the characteristics of peripheral stimuli with great fidelity are suppressed during the movement task (possibly the case for the sample of area 1 neurons with cutaneous RFs). This hypothesis would seem more reasonable if it could be demonstrated that cutaneous RF neurons whose activity is entrained to the stimulus frequency or that have RFs in direct contact with the handle are not suppressed whereas those that are not entrained or have RFs away from the point of contact are less responsive in the movement task. This hypothesis is currently under investigation, yet it does not explain why the activity of deep RF neurons in area 3a, 3b and 1 and the activity of area 3b cutaneous RF neurons is enhanced during movement trials. Inputs from deep receptors may be enhanced because they signal the current state of limb position prior to the execution of movement and are thus behaviorally important.

This work has been submitted for publication in *Brain Research Bulletin.*

2) <u>The Multimodal Experiments</u>

These experiments were designed to test the hypothesis that a certain portion of the activity that vibratory responsive neurons exhibit just prior to movement onset represents a "reactivation" of their sensory response. We also sought to determine if the reactivated sensory response was attenuated at this time and if the another component of the premovement activity was also attenuated, suggesting that both peripheral and central inputs may partially or completely "gated-out" before movement.

Summary of Findings

When monkeys make wrist movements in response to vibration of their hands, primary somato-sensory (SI) cortical neurons that adapt quickly to the vibratory stimulus often exhibit two temporally separate types of activity. Initially, these neurons respond to the stimulus. They then cease discharging, only to resume firing prior to the movement. This activation, cessation and reactivation occurs even though the sensory stimulus remains on until after the movement is begun. The first change in activity is most likely related to sensory input. The second, which has been called premovement activity, may have a sensory component as well as one related to the upcoming movement. We wanted to test the hypothesis that the premovement activity exhibited when vibration is present represents both a reactivation of a neuron's vibratory response and the premovement activity

that normally occurs when vibration is absent. We also wanted to determine if neurons in areas 3b and 1 show similar or different activity patterns during the initiation and execution of sensory triggered wrist movements. Four monkeys were trained to make wrist flexion and extension movements in response to vibratory stimuli delivered to the handle which the animals used to control the behavioral paradigm. Two of the four monkeys also made similar wrist movements following visual cues.

We found that the premovement activity of quickly adapting neurons located in area 1 (but not area 3b) is comprised of a sensory-related component as well as a movement-related component. The magnitude of these individual components differs in relationship to a neuron's receptive field type, the movement direction and the external force imposed on the stimulated forelimb. Premovement activity of area 3b and area 1 neurons occurs at the same time prior to movement, regardless of whether visual or vibratory cues are used to trigger wrist movements. This activity occurs at about the same time as others have observed elevations in the threshold for tactile perception, suggesting that premovement activity and changes in sensory responsiveness before movement may be related.

These and previous findings are used to construct a model which may predict the firing patterns of SI quickly adapting neurons during behavioral tasks. These findings also suggest that areas 3b and 1 may have different roles in processing task-related somatosensory information.

Results

Recordings from 166 area 1 and 61 area 3b neurons were initially examined. All neurons included in this study met certain selection criteria. Each exhibited a short latency (often less than 50 ms) phasic response associated with vibratory stimulus onset. Each then showed a decrease in activity from the level associated with stimulus onset, often returning to near background levels. Each also had a change in activity that occurred prior to movement onset. Therefore, each had a clear separation between stimulus- and premovement-related activity. Finally, each neuron had a peripheral receptive field that was located on the hand or the wrist of the forelimb that was used to make the behavioral response. Neurons with cutaneous and deep RFs were analyzed separately.

The recordings of the area 3b and 1 neurons were separated into individual "cases" for several reasons. First, the activity of many neurons was studied based on the use of more than one vibratory stimulus frequency. The stimulus-related and premovement activity changes of these neurons were not always identical during blocks of trials at different stimulus frequencies. Second, two different movements were required. Flexion movements were made against a load, whereas extension movements were assisted by the same load. A case was defined as the recordings from a neuron using only one vibratory stimulus and requiring a movement in one direction. No more than 3 cases from an individual neuron were included in any single data group described below. From the SI neurons listed above, we examined 339 area 1 cases and 130 area 3b cases. A total of 234/339 (69%) of the area 1 and 94/130 (72%) of the area 3b cases were vibratory responsive. Of these, 133/234 (57%) and 57/94 (61%) area 1 and area 3b cases, respectively, met the remaining selection criteria. A total of 96/133 (72%) of the area 1 and 29/57 (51%) of the area 3b cases recorded from two monkeys had a sufficient number of visually cued trials to enable the determination of premovement activity associated with similar movements made in the absence of vibratory stimuli. Table 2 shows the distribution of these cases by cortical location, RF type and peripheral location of the RFs. Figure 2 illustrates the task-related activity of an area 1 neuron that met the selection criteria. It had a short latency phasic response to the onset of vibration and a nonstimulus-related change in activity that occurred prior to the onset of movement.

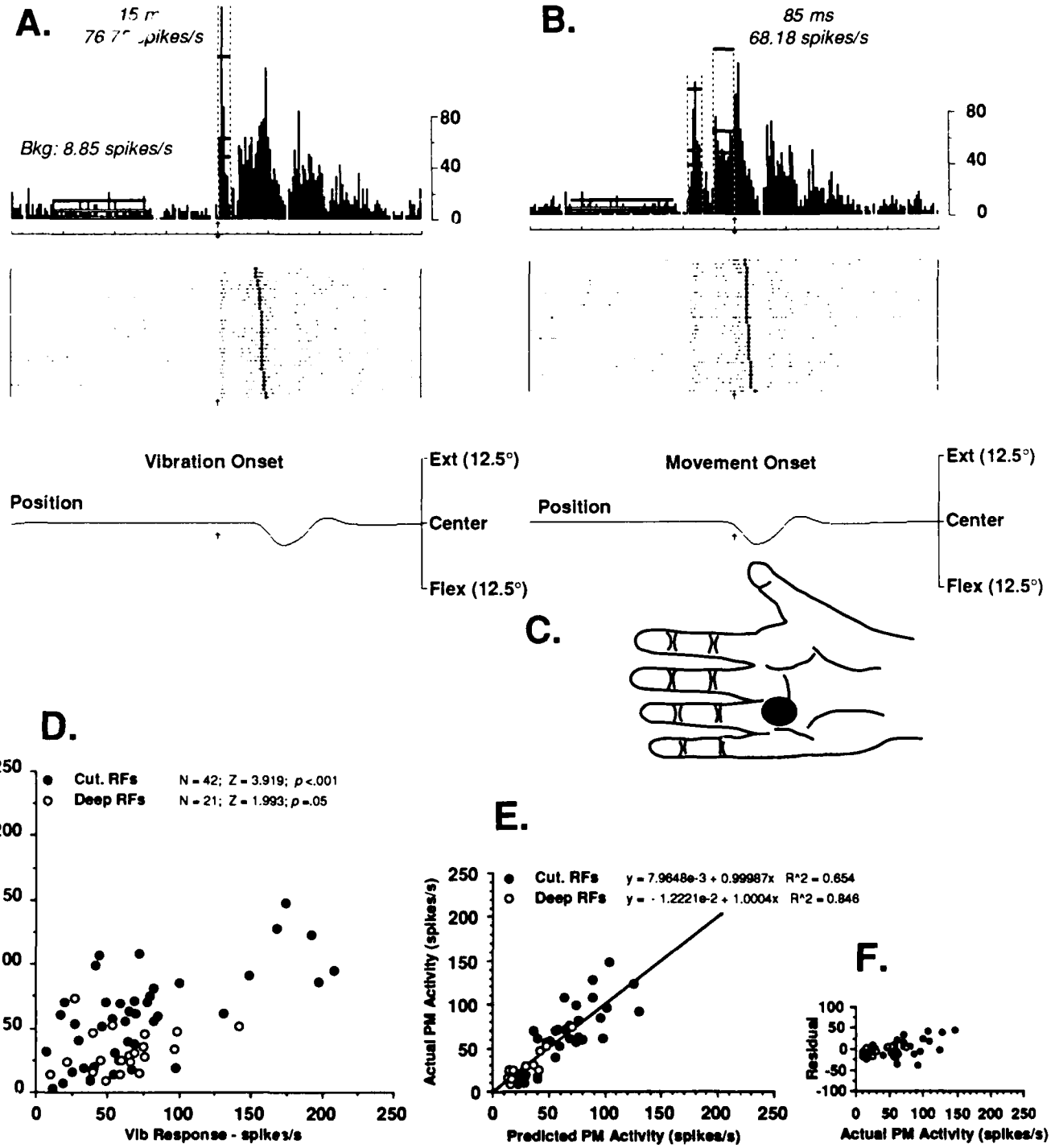


Figure 2. A. and B. Rasters, histograms of the task-related activity of an area 1 neuron along with associated average wrist position traces. C. This neuron's cutaneous receptive field. A.trials centered on vibration onset and ordered by reaction time (dark marks in the rasters signify movement onset). Background activity and the stimulus-related changes in discharge rate and onset times are listed. B. the same trials centered on movement onset. Trials ordered by movement time. The dark marks indicate reward, a 5° movement and the cessation of the vibratory stimulus. Horizontal open lines in each panel indicate the upper and lower thresholds and mean values for the background activity, vibratory response and premovement activity. Vertical dashed lines show the onset and offset of stimulus-related activity (A. and B.) and premovement activity (B). The full span of displays is 2 s. D. Scattergram of the magnitude of mean vibratory stimulus-related activity (Vib response) vs. the magnitude of the mean premovement [PM] activity for area 1 neurons, expressed in spikes/s. Each panel indicates the number of cases analyzed, the correlation coefficient, and the probability that the correlation was significant. E. Scatterplot of the actual premovement activity (PM) recorded in vibratory-cued trial vs. the predicted PM activity obtained by using the coefficients listed in Table 4 and equation 1. Cases are separated by receptive field type, direction of the movement madefor area 1 neurons. Regression equations are shown in the upper right-hand corner, along with the multiple regression coefficients indicating of the goodness of fit. Inset scattergram (F) plots the actual PM against the residuals remaining from the application of equation 1 to recorded values using the coefficients listed in Table 3. No significant trends were evident in the residuals.

Table 2: Distribution of cases

	Area 3b				Area 1			
	QA Vib		Vis. Trials		QA Vib.		Vis. Trials	
Cutaneous RFs	38	(67%)	13	(23%)	77	(58%)	60	(45%)
Digits								
Ventral	3	(5%)	1	(2%)	28	(21%)	24	(18%)
Dorsal	4	(7%)	2	(4%)	0	(-)	0	(-)
Hand								
Ventral	22	(39%)	1	(2%)	40	(30%)	28	(21%)
Dorsal	1	(2%)	1	(2%)	4	(3%)	4	(3%)
Wrist								
Ventral	3	(5%)	3	(5%)	4	(3%)	4	(3%)
Dorsal	5	(9%)	5	(9%)	1	(1%)	0	(-)
Deep RFs	19	(33%)	16	(28%)	56	(42%)	36	(27%)
Digits								
Flex	0	(-)	0	(-)	9	(7%)	5	(4%)
Ext	14	(24%)	13	(23%)	20	(15%)	12	(9%)
Wrist								
Flex	3	(5%)	3	(5%)	9	(7%)	6	(4%)
Ext	2	(4%)	0	(-)	18	(13%)	13	(10%)

Table 2. The distribution of cases by cortical location, RF type and RF location. Percentages are of total populations of area 3b (N=57) and area 1 (N=133) cases. QA Vib; all cases. Vis. Trials; those cases with sufficient visually cued trials for statistical comparison with vibratory cued trials.

Table 3: Mean Premovement Onset Times (ms)

Condition	Vib Trials	SD	Vis. Trials	SD	Δ Vib/Vis
Area 1					
Flex-Cutaneous (N=33)	75.0	32.1	75.6	31.7	n.s.
Flex-Deep (N=13)	98.8	27.3	81.9	23.2	.014
Ext-Cutaneous (N=27)	72.8	24.9	73.9	28.3	n.s.
Ext-Deep (N=23)	90.2	29.2	82.4	26.8	n.s.
Area 3b					
Flex-Cutaneous (N=6)	51.7[a]	19.6	40.0[b]	17.6	n.s.
Flex-Deep (N=10)	125.0	61.1	127.0[a]	48.9	n.s.
Ext-Cutaneous (N=7)	73.6	42.6	69.3	15.1	n.s.
Ext-Deep (N=6)	83.3	20.4	88.3	32.0	n.s.
Population	83.0	35.8	79.8	33.6	n.s

Different from population values, [a] : $p < .02$; [b] : $p < .005$.

Table 3. The mean onset times of premovement activity for SI neurons indicated in ms prior to movement onset. Shown are the means and standard deviations (SD) for these neurons separated by cortical location, the type of movement made, and their receptive field type. The right column indicates the significance (n.s; not significant) of the difference between the mean premovement activity onset during vibratory as compared with visually cued trials. In only one instance were these onsets significantly different.

Premovement Activity Onset

We calculated the onset of activity that occurred before a movement but that was not temporally associated with the onset of vibratory stimuli (premovement activity). In a previous report (Nelson 1987), we argued that premovement activity occurring earlier than 61 ms before movement onset might be the result of central rather than peripheral inputs. The majority of studied neurons had early premovement activity changes. For area 1, 69% and 86% of the neurons with cutaneous and deep RFs, respectively, increased activity earlier than 61 ms before the movement began. For area 3b, 71% and 95% of neurons with cutaneous and deep RFs, respectively, showed early premovement activity.

The onset times for the premovement activity were compared for those cases in each group where sufficient visually cued trials were recorded to determine if the activity onset differed as a function of cortical location, type of movement made, and type of RF. Table 3 shows that for all but one data group, these onset times were not significantly different ($p >> .05$; paired t-test). During the performance of flexion movements, area 1 neurons with deep RFs had premovement activity that occurred earlier for vibratory than for visually cued trials (mean difference 17 ms; T = 2.856; DF =12; $p = .014$). In general, area 3b and 1 neurons with deep as compared with cutaneous RFs had premovement activity which occurred earlier, regardless of the type of sensory cue used. While this trend existed for area 1 neurons, the onset times were not significantly different from the population mean. Table 3 shows that some values for the premovement activity onsets of area 3b neurons were significantly greater or less than the population means. It should be noted, however, that the sample size of area 3b neurons is small. With larger area 3b sample sizes, the values may differ as well as their relationships to the population means.

Correlation between Vibratory Responsiveness and Premovement Activity Magnitude

The vibratory responsiveness of SI neurons was compared with the magnitude of their premovement-associated discharge to determine if the magnitudes of these two activity changes were correlated. The data were grouped by the cortical area in which the neurons were recorded, the movement direction (wrist flexion or extension) ,and the RF type (either cutaneous or deep).

The magnitude of the stimulus response was plotted against the magnitude of the change in premovement activity for each case grouping. Nonparametric correlation analyses were performed on each case grouping of area 3b and 1 neurons. Spearman Rank Correlation analyses were conducted because there was no *a priori* reason to assume that the relationships between sensory responsiveness and premovement activity would be linear, or that the measures would be normally distributed. An examples of one of these plots are seen in Figure 2D.

The magnitude of the premovement activity was positively correlated with the magnitude of the vibratory response for area 1 neurons having either cutaneous or deep receptive fields during flexion movements. These movements were against the load and in the direction of the stimulated surface of the hand. For extension movements, which were away from the stimulated hand surface and assisted by the load, only the area 1 neurons with cutaneous RFs showed a positive correlation between vibratory responsiveness and premovement activity magnitude. The premovement activity of deep RF area 1 neurons during extension movements was negatively correlated with vibratory responsiveness. The correlation coefficients for each group of area 1 neurons were statistically significant ($p <= 0.05$) with two of the four case groupings (those with cutaneous RFs) showing a more reliable correlation ($p < 0.001$). The vibratory responsiveness of area 3b neurons was not correlated with the premovement activity for any of the stimulus-movement combinations.

Relationships between Vibratory Responsiveness and Premovement Activity Magnitude

The data from recordings where more than 20 vibratory and visually cued trials each were conducted were analyzed further. These data were standardized and examined using factor and multiple regression analyses to determine if premovement activity during vibratory cued trials was statistically dependent upon the vibratory responsive of the neurons. Standardization consisted of determining the mean activity for each measured parameter and then translating the actual activity values to Z-scores. Principal components factor analysis indicated that 65-84% of the variance in the area 1 premovement activity during vibratory cued trials could be accounted for by just two factors: the vibratory responsiveness of the neurons and the premovement activity exhibited during visually cued trials (when vibration was absent). The weightings of these analyses suggested that the following equation provides a good description of the data:

$$\textit{Vib trial PM activity} = \textit{constant} + \alpha * \textit{vibratory responsiveness} + \beta * \textit{visual trial premovement activity} \quad (1)$$

where α represents some portion of the magnitude of the neuron's initial vibratory response, β is some portion of the premovement activity magnitude exhibited in visually cued trials, and the constant indicates the activity not accounted for by the other two terms.

We assumed that the visual trial premovement activity reflects a neuron's capacity for movement-related activity when vibration is not present. We also assumed that the vibratory responsiveness is reflected by the initial activity associated with the onset of the vibratory stimulus. Finally, it was necessary to determine that visual trial premovement activity was independent of the vibratory responsiveness of the neurons. For area 1, vibratory responsiveness was not correlated with visual trial premovement activity ($p > .05$; Spearman Rank Correlation Test). For three of the four groups of area 3b neurons, this was also true. The fourth group (neurons with deep RFs, extension trials) showed a statistically significant correlation between these two measures ($p = .02$). For area 3b neurons, three of the four case groups had a significant correlation between the premovement activity in vibratory as compared with visually cued trials. No group showed a correlation between vibratory responsiveness and vibratory trial premovement activity, as stated above.

Predictions of the premovement activity for each behavioral condition were made using the results of multiple regression analyses (equation 1) for area 3b and 1 neurons. The coefficients derived from these analyses using the model equation are listed in Table 4. For area 1 neurons with cutaneous RFs, the premovement activity in vibratory-cued trials was always predicted by some portion of the vibratory responsiveness of the neurons (0.41- 0.57) and some portion of the premovement activity exhibited in visually cued trials (0.49-0.56). Area 1 neurons with deep RFs had a different relationship between premovement activity and sensory responsiveness. During flexion trials, when the movement to be made was in the direction of the stimulated surface of the hand and opposing the load, the premovement activity in vibratory-cued trials was predicted by 0.53 times the vibratory responsiveness component and 1.2 (not statistically different from 1.0) times the magnitude of the premovement activity recorded in visually cued trials. When movements were made away from both the load and the stimulated surface of the hand (extension), the coefficient for the vibratory component was not different from 0.0 and that for the visual trial premovement component was not different from 1.0. For area 3b, the vibratory responsiveness term was never significantly different from 0.0. The coefficient of the visual trial premovement component could be set to 1.0. These results for area 3b

Table 4: Coefficients for Equation 1

Condition	Constant	α	β	R^2
Area 1				
Flex-Cutaneous (N=33)	0.0	0.572[a]	0.498[a]	0.654
Flex-Deep (N=13)	0.0	0.535[a]	1.200[b]	0.846
Ext-Cutaneous (N=27)	0.0	0.410[a]	0.558[a]	0.755
Ext-Deep (N=23)	0.0	0.098[c]	0.946[b]	0.839
Area 3b				
Flex-Cutaneous (N=6)	0.0	-0.422[c]	0.661[b]	0.818
Flex-Deep (N=10)	0.0	-0.002[c]	0.977[b]	0.951
Ext-Cutaneous (N=7)	0.0	0.273[c]	0.969[b]	0.847
Ext-Deep (N=6)	0.0	0.016[c]	0.983[b]	0.997

Table 4. The results of regression analyses using equation 1. Listed are the relationships derived from only those neurons for which a full set of vibratory and visually cued trials was recorded. Columns list the standardized constant, coefficients and R^2: a measure of the variance accounted for by the regression equations. Symbols: [a] = different from 0.0 and 1.0; [b] = different from 0.0 but not from 1.0; [c] = not different from 0.0 yet different from 1.0. Probability level for significance, .01. Conditions list the direction of movement and the type of receptive fields which these neurons have.

neurons could, in part, be due to the small sample size. We also calculated the regression coefficients for reduced populations of area 1 cases (those recorded during trials using 57Hz vibratory stimulation only). The regression coefficients for all case groups were not statistically different than those for the larger populations.

The coefficients listed in Table 4 were used to calculate the predicted value of the vibratory trial premovement activity. This value was then compared with the actual data. An example of the predicted versus the actual premovement activity using equation 1 for area 1 neurons can be seen in Figure 2E. The linear fit of the actual data to the values calculated using equation 1 suggests that this equation is a reasonably good predictor of the relationships between the premovement activity during visually and vibratory-cued trials and the responsiveness of area 3b and 1 cortical neurons to vibratory stimuli. The lack of trends in the residuals from the application of this equation to the actual data (Figure 2F) suggests this as well.

A Reactivation and Premovement Activity Model

These observations suggest to us a model (Figure 3) which may account for the activity of quickly adapting area 1 neurons during task performance. We have used the characteristics of area 1 quickly adapting neurons with deep RFs to construct this model. Next, we have removed some model elements to explain the activity of neurons in area 3b and area 1 neurons with cutaneous RFs.

Using the model, we can predict the activity of model components which, when taken together, could account for the firing patterns observed for the studied quickly adapting area 1 neurons with deep RFs. A sustained sensory input (SV), in this situation vibratory stimulus-associated, may interact with a task phase input (TP) which occurs once the stimulus is perceived as being the go-cue and suppresses the stimulus-associated activity at the sensory summing point (SS). When the motor command signal associated with movement initiation (NM) occurs, it may impinge upon both the

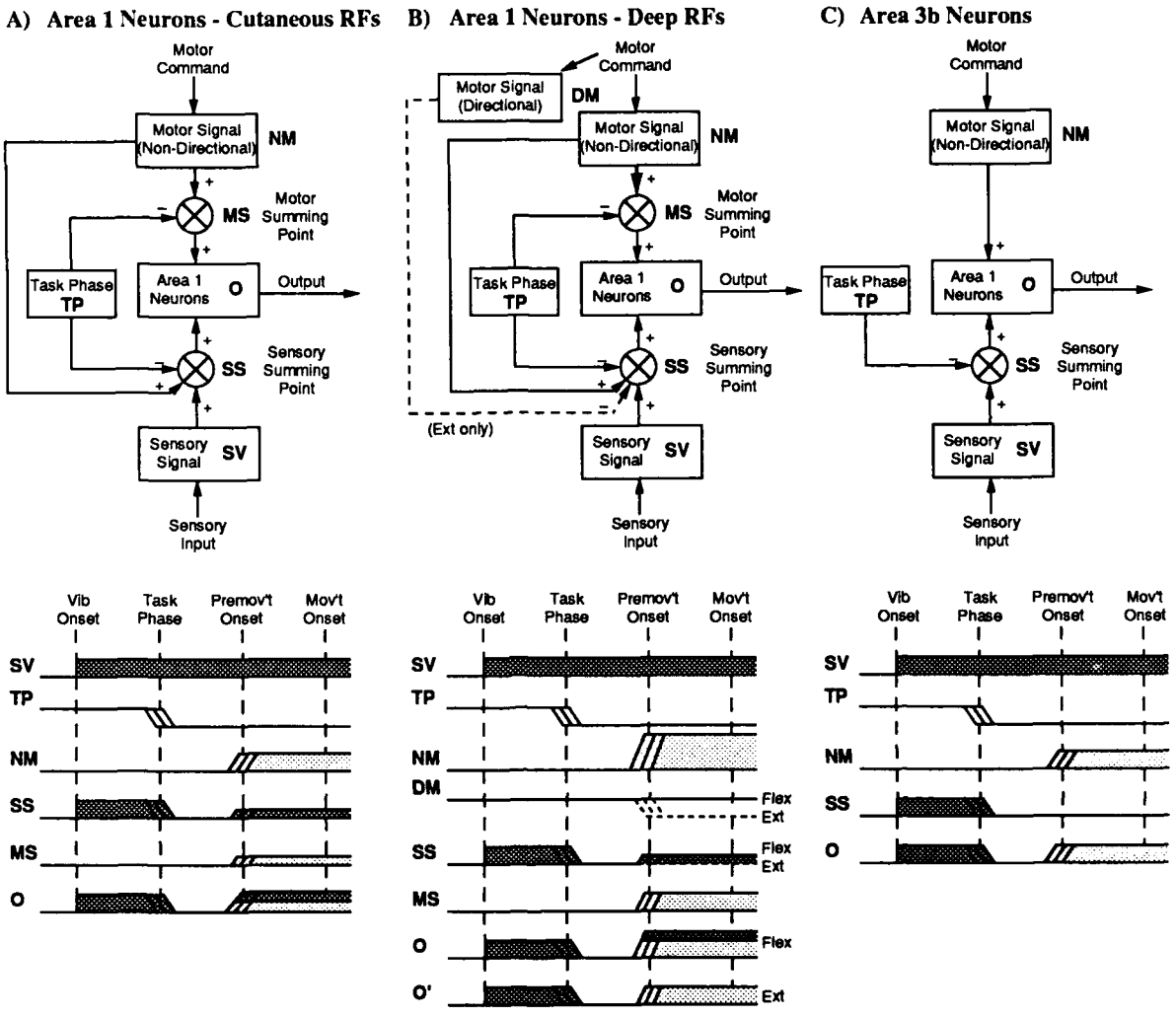


Figure 3. A model which may account for the activity of SI neurons with phasic vibratory responses during task performance. Each variation of the model has several components in common. These include: a sustained sensory input associated with peripheral vibratory stimulation (SV); a task phase component which changes state once the appropriate trigger stimulus is perceived (TP); a non-directional motor signal associated with the initiation of movement (NM); a summing point where SV and TP interact (SS); and the output of the quickly adapting neurons (O or O'). For area 1 neurons (panels A and B), a summing point (MS) is added where the task phase input interacts with the non-directional motor signal (NM). For area 1 neurons with deep RFs (panel A), a directional motor signal (DM) is added which interacts at the sensory summing point (SS). Interactions of these components are depicted at four arbitrary points in time (horizontal axes of lower portions of each panel). These points are: at go-cue presentation (Vib Onset), once the stimulus is perceived (task phase), at the initiation of the movement (premovement onset) and at the movement's execution (movement onset).

sensory (SS) and motor (MS) summing points. We assume that this signal partially overrides the suppression exerted by the task phase input (TP) at both summing points. We predict this would result in a partial reactivation of the vibratory response and activity associated with the initiation of movement being present at the summing points. Our observations, however, would suggest that vibratory response reactivation does not always occur. To account for this, we postulate that a directional motor signal (DM) also interacts at the sensory summing point (SS), suppressing reactivation of the sensory response before flexion but not extension movements. The interaction of the summed sensory and motor inputs to area 1 quickly adapting neurons with deep RFs could result

in the activity patterns depicted. Before flexion movements, the premovement activity (O) would consist of a reactivation of the vibratory response (although attenuated) and a motor component. Prior to extension movements, the premovement activity (O') would reflect the motor component alone, as observed. This model is shown in Figure 3, panel B.

The model can be simplified to account for the observed activity of the other SI quickly adapting neurons. For area 1 neurons with cutaneous RFs (panel A), removal of the directional motor signal (DM) could result in premovement activity consisting of an attenuated reactivation of the vibratory response and an attenuated signal associated with the initiation of movement. For area 3b neurons (panel C), removal of the non-directional motor signal (NM) from the sensory summing point (SS) and both the directional motor signal (DM) and the task phase signal to the motor side of the model could account for premovement activity. In this case, the premovement activity prior to movements in either direction for neurons with deep or cutaneous RFs would reflect only the component associated with movement initiation.

Conclusions

Reactivation of the sensory response occurs before movement in area 1 but not area 3b SI neurons. Another component of the premovement activity, one presumably coming from motor centers may also be attenuated depending upon cortical location of the neurons and RF type.

There are several possible functional roles for SI quickly adapting neurons with premovement activity and sensory response reactivation. The interpretation we favor is that SI neurons of the type reported here may be involved in modulating sensory responses of other neurons. Previously it has been suggested that premovement activity in SI neurons may be a result of a corollary discharge. This discharge, presumably coming from motor centers, could interact with ascending somatosensory transmission at the levels of the dorsal column nuclei, thalamus and at the level of the cortex itself. We assume that ongoing vibratory input to quickly adapting neurons has two distinct roles in the tasks used in this experiment. Initially, it serves as the go-cue and its detection has obvious behavioral importance. However, at the time that the instructed wrist movement is about to begin, this peripheral vibration may actually interfere with the monkey's ability to execute wrist movement since vibration can activate the same receptors used to provide feedback about this movement.

Changes in sensory responsiveness, which are perhaps mediated by the studied neurons, might actually be part of an attentional system. Premovement activity and reactivation of the vibratory response may indicate a shift in the behavioral importance from vibration as a go-cue to vibration as a peripheral stimulus that is no longer important for the task since it has already been perceived. At stimulus onset, the output of quickly adapting neurons may serve to increase the "signal to noise ratio" of a class of go-cue responsive neurons by suppressing other sensory inputs which do not signal the presence of the go-cue with great fidelity. Before movement, the output of these quickly adapting neurons may reflect additional changes in sensory responsiveness associated with a shift in attention toward the behaviorally important inputs from peripheral sensory elements involved in monitoring movements and away from inputs carrying information that has already been processed or that may interfere with the monitoring itself.

This work was initially reported in the Annual Technical Report for the first year of this grant. The analysis these data and their implications have undergone significant revision since that report. These findings have been submitted for publication in ***Experimental Brain Research.***

3) The "Unexpected Failure" Experiments

This experiment was designed to test the hypothesis that variations in expectation alter the sensory responsiveness and the magnitude of premovement activity exhibited by SI cortical neurons. By using a pseudo-random reward schedule for correct task performance, we sought to create a condition under which monkeys sometimes were not reinforced for seemingly appropriate movements. Several types of results were thought to be possible. In trials immediately following correct but unrewarded performance ("after trials"), both sensory responsiveness and premovement activity may be either enhanced or suppressed.

Summary of Findings

In this pilot experiment, one monkey was trained to make wrist flexion and extension movements in response to vibratory go-cues, as previously described. Approximately 75% of the trials in which the monkey performed correctly were rewarded. The other 25% were not. The activity patterns of 18 task-related neurons have been recorded to date. From preliminary observations, it appears that during behavior, when the outcome is predictable (i.e., when the monkey has previously been rewarded for performing correctly) both sensory responsiveness and premovement activity in SI neurons are at one level. In trials which follow the withholding of the reward for correct performance, and hence the outcome is unpredictable, sensory responsiveness is enhanced. Premovement activity is also enhance under the unpredictable condition for the majority of the studied neurons. This suggests that during behavior with a predictable outcome, neuronal responsiveness to peripheral and central inputs is partially attenuated, whereas when behavioral conditions become unpredictable, neuronal responsiveness is not gated, but rather, is enhanced.

Results

The distribution of unrewarded trials was determined by a pseudo-random number generator with no apparent sequential order in the output. Upon detecting the go-cue during in the after trials, the monkey typically made movements in the opposite direction from the rest of the trials in that block .

Neuronal activity during rewarded flexion trials was compared with that for after trials in which the monkey also flexed his wrist. Corresponding rewarded and after extension trials were also compared. The recordings were separated into cases for the same reasons discussed previously (see *The Multimodal Experiments*). This separation resulted in a total of 26 cases from 14 neurons which, because of their stereotaxic location, are believed to be located in SI. No single neuron's data contributed more than 2 cases to the data population. Histological confirmation of the neurons' locations awaits the termination of these ongoing experiments.

To date, the vibratory stimulus-related responses and/or premovement activity magnitudes have calculated for all 14 neurons. The activity patterns of one of these neurons can be seen in Figure 4. Of the 26 resulting cases, 24/26 (14 neurons) had enough trials for both the rewarded and after conditions for the premovement activity to be calculated. Sufficient trials in both condition were recorded for 12/26 cases (7 neurons) that were vibratory responsive. The vibratory response for the rewarded trials was compared to the vibratory response during the after trials for each case. A paired *t*-test was conducted to determine if the neurons were more vibratory responsive in one type of trials as compared with the other. During the rewarded trials, the neurons as a population were less responsive to vibratory stimuli as compared with during the after trials (DF=11; Mean difference: -8.09 spikes/s;

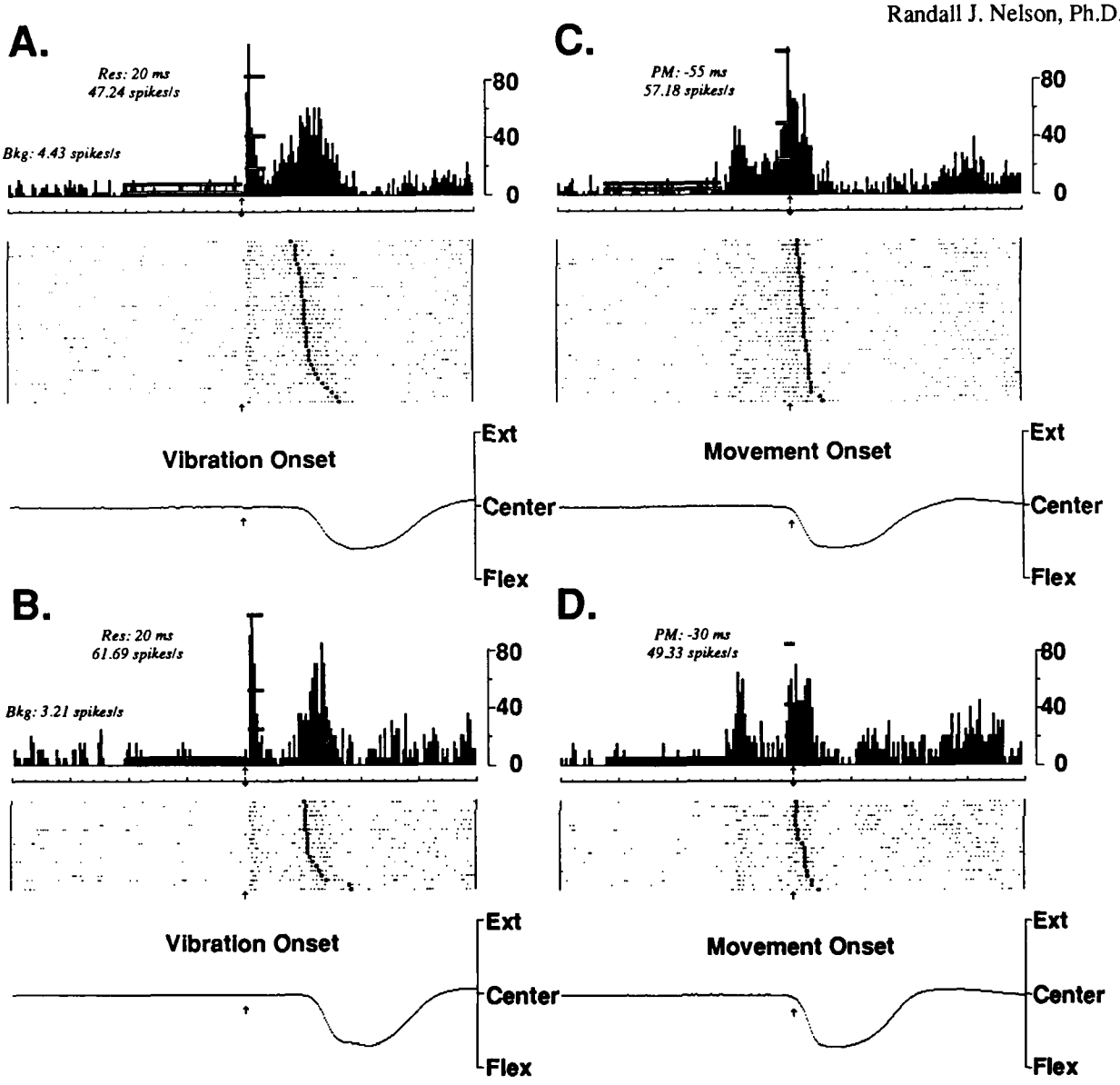


Figure 4. General description of panels as in Figure 1. The vibratory response related activity of a presumptive SI neuron for rewarded trials (A.) and after trials (B.). Traces centered on stimulus (57Hz vibration) onset. Listed are the background (Bkg) activities and the mean magnitude of the responses above background in spikes/s. Also listed are the onsets of response related activity. Panels (C.&D.) show the same trials centered on movement onset. Listed are the premovement (PM) activity magnitudes above background and their onsets before movement. This neuron was more responsive to vibration in the after trials than in the regular rewarded trials. The premovement activity was smaller in the after trials as compared with the regular rewarded trials.

t=-1.995; p<.05; one-tailed). The premovement activities for the two types of trials were also compared. When the total population of 24 premovement activity cases was analyzed, the pre-movement activities under the rewarded and after conditions were not significantly different (DF=23; Mean difference: 1.97 spikes/s; t=-.492; p>>.05; one-tailed). The data were subjected to cluster analysis which resulting in the population being split into two groups. The first group consisted of 20 cases (from all 14 neurons), and was evenly mixed with flexion and extension movement cases. For

this group, the premovement activity during rewarded trials was less than during after trials (DF=29; Mean difference: -4.76 spikes/s; t=-1.78; p<.05; one-tailed). The second group consisted of 4 cases (from 4 neurons) all of which were recorded during extension movements. For this group, the premovement activity during rewarded trials was much greater than during after trials (DF=3; Mean difference: 35.6 spikes/s; t=-4.69; p<.01; one-tailed).

It should be restated that these experiments are currently being conducted, that the sample size is small, and the cortical locations of the recorded neurons are unconfirmed.

Conclusions

Despite the small sample size, it appears that SI neurons are more responsive to vibratory inputs during unpredictable as compared with predictable behavioral conditions. Moreover, most of the studied neurons appear to have more premovement activity, which is believed to result from central inputs, when conditions are unpredictable. These observations suggest the following working hypotheses. Sensory responses are elevated during unpredictable behavior conditions so that a greater amount of sensory information can be processed, lest important inputs not be detected. Prior to movement, premovement activity (which may contribute to the gating out of extraneous inputs) is elevated to keep unimportant inputs from interfering with the monitoring of that movement. These thoughts are in keeping with our previous suggestions about the role of premovement activity and shed new light on the nature of enhancement and suppression of sensory responsiveness is they occur under different behavioral conditions.

4) The Target Reaction Time (RT) Experiments

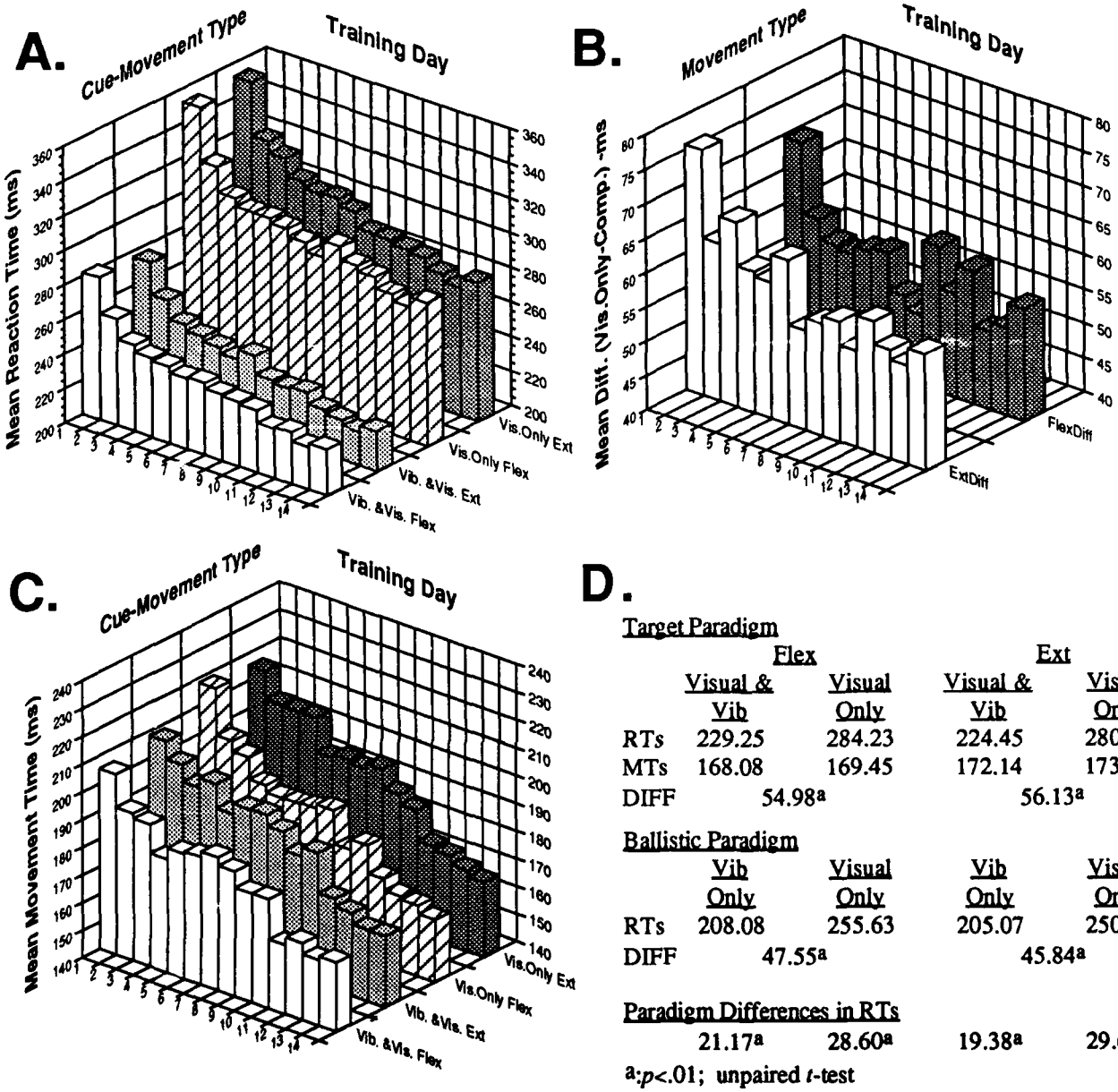
This study was carried out to test the hypothesis that wrist movements made from a centered position to acquire a visual target would occur more quickly if, in addition to the illumination of the target, subjects also received a vibratory stimulus, indicating that a movement should be made.

Summary of Findings

Nine human subjects made movements from a centered wrist position to a target 5° from the center position by either flexing or extending the wrist of their preferred hand. Two "go-cues" were used to indicate that a movement should begin. The first consisted of illuminating a target LED on the visual display that would be illuminated if the subject made a 5° movement in the appropriate direction. The second consisted of the target *and* a vibratory stimulus delivered to the palm of the hand that was to be moved. Subjects as individuals and as a group always began movements more quickly after the visual plus vibratory cue (combined cue) than after the visual cue only. From the first training day and for two weeks thereafter, RTs for the combined cue trials were significantly faster (as measured by a paired t-test) than for the visual cue only trials. RTs and movement times (MTs) improved throughout training. However, for individual subjects and for the group as a whole, mean MTs for a given training day were not significantly different in relationship to movement direction or cue type. These results suggest that precise movements to a visual target are begun more quickly when vibration of the hand to be moved is used in addition to target illumination as go-cues for movement.

Results

The RTs and MTs for small (5°) controlled movements were measured. Subjects were initially told that they should make flexion or extension movements as quickly as possible from a centered wrist



D.

Target Paradigm

	Flex		Ext	
	Visual & Vib	Visual Only	Visual & Vib	Visual Only
RTs	229.25	284.23	224.45	280.58
MTs	168.08	169.45	172.14	173.51
DIFF	54.98[a]		56.13[a]	

Ballistic Paradigm

	Vib Only	Visual Only	Vib Only	Visual Only
RTs	208.08	255.63	205.07	250.91
DIFF	47.55[a]		45.84[a]	

Paradigm Differences in RTs

	21.17[a]	28.60[a]	19.38[a]	29.67[a]

[a]: $p<.01$; unpaired t-test

Figure 5. (A) The mean RTs by training day, separated by cue-movement type. (B) The differences in mean RTs for extension and flexion movements calculated by subtracting the mean RTs for the visual & vibratory cued trials from the mean RTs for visual cue only trials. (C) The mean MTs by training day, separated by cue-movement type. (D) The final RTs and MTs for the target paradigm and for the ballistic movement paradigm. Shown also are the differences in RTs for corresponding cue-movement types for the two paradigms.

position to a position indicated by target LEDs (target acquisition). These LEDs were part of the visual display described previously. Subjects were instructed not to sacrifice position accuracy for movement speed. They were also told that, while they would always be presented with a target indicating in what direction and how far they should move, sometimes the illumination of the target would be accompanied by vibration of the handle in which their hand rested. Combined cue and visual only trials were presented randomly in each block of 10 trials. The movement direction was alternated from block to block beginning with a request for flexion movements.

Daily mean RTs and MTs were calculated from 360 extension and 360 flexion trials that subjects ran during each session. Each subject performed the paradigm for 14 days. Figure 5A shows the average daily mean RTs for each training day. These were calculated by averaging the daily mean RTs for all subjects for a given training day. Daily RTs for combined cues trials for either movement direction were always significantly faster ($p<.01$; paired two tailed t-test) than the corresponding trials cued by the target alone (visual only). The daily differences in RTs for corresponding movements are shown in Figure 5B and ranged from 50-70 ms. The differences in RTs became less with practice; i.e., more days of training. MTs also improved with training (Figure 5C). However, the MTs for the four cue-movement groups were never significantly different on a given training day. The daily mean RTs and MTs from each subject for the last 5 training days were used to calculate each subject's final means. These final means were used to calculate grand average RTs and MTs (Figure 5D). The differences in the grand average RTs were calculated by subtracting the grand average RTs for the combined cue trials from those for trials using the visual cue only. These differences were approximately 55-56 msec in favor of the combined cue trials and were significantly different ($p<.01$; unpaired two tailed t-test).

The final mean RTs from the nine subjects who performed the target paradigm were compared with the final RTs recorded from ten subjects that made ballistic movements (i.e., amplitude not restrained but >5°) in response to either vibratory or visual cues (Nelson et al., 1990; see List of Publications). The vibratory cued RTs from the ballistic paradigm were compared with the combined cue RTs from the target paradigm. The visually cued RTs from the ballistic paradigm were compared with the target only RTs from the target paradigm. When vibration was present, the RTs in the target paradigm were approximately 20 ms slower than in the ballistic paradigm. When vibration was not used a cue (visual only trials), the RTs for the target paradigm were approximately 30 ms slower than in the ballistic paradigm.

Conclusions

Movements to acquire a target are made more quickly if a vibratory go-cue is presented in addition to the illumination of the target. Previously we have shown that ballistic movement are made more quickly in response to vibratory as compared with visual go-cues. The differences in RTs observed in these previous experiments also appear to occur when instead of unrestrained movement, subjects must make controlled movements of small amplitude. Once controlled movements are begun, the time to target acquisition (movement time) does not vary significantly regardless of whether low amplitude vibration is present or absent. Increased practice shortens RTs and MTs. Vibratory stimuli in addition to other visual cues could significantly increase performance as measured by shorter RTs. It remains to be determined whether vibratory go-cues are beneficial in situations requiring more precise movement control and with more sensory stimuli competing for a subject's attention.

General Statement

The overall goal of the research conducted by this laboratory is to understand the role that behavioral contingencies play in regulating the responsiveness of neurons that are involved in the control of wrist movement. Advances in this understanding make two contributions; the first to our general understanding of how the primate nervous system functions and the second to practical applications for device control.

We have chosen to study SI neurons because of our expertise with these neurons and because of their pivotal position in sensorimotor integration that ultimately results in controlled, goal-oriented behavior. It was previously thought that the responsiveness of SI neurons to peripheral and central inputs was essentially unaltered by behavioral contingencies. Findings from this laboratory and others have suggested that SI neurons undergo sometimes profound and sometimes subtle changes in responsiveness to both peripheral and central inputs. These findings have implications for the understanding of motor control because SI neurons provide direct or indirect inputs concerning limb position and muscle tension to other cortical regions such as posterior parietal, motor, premotor and supplementary motor cortices, as well as to the basal ganglia. All of these structures have been implicated in the control of movement. The demonstration of changes in the responsiveness in SI neurons then implies that the regions mentioned above may receive "pre-processed" information that differs depending upon the behavioral conditions present at any given time. Clearly, to understand motor control, the factors that influence it must be understood, and thus an understanding of the contributions which SI makes to this control are of great importance.

The practical application of this understanding may lead to more efficient design of control systems which utilize changes in wrist position. The results of human psychophysical experiments suggest that the timing of wrist position controlled target acquisition may be improved without any degradation in movement performance or accuracy. Caution is warranted and further studies are needed, however, because it has been established that vibratory stimuli can adversely effect wrist position control if the signals are of great enough amplitude.

Status of Future Research

We are in the process of recording from a monkey who was trained to perform the "Unexpected Failure" Paradigm. We will continue to do so during year 03 of this grant and plan to record from a second animal trained to perform the same task prior to the termination of USAF GR AFOSR 88-0179.

We have two sets of human psychophysical experiments planned. In the first, we will randomly vary the amplitude of movement required (5°, 10° or 15°) by using different target lamps using visual only or visual plus vibratory go-cues. This will be done to determine if the RT differences between to two trial types remain constant with altering amplitudes of required movement. We will also measure MTs to determine the relationship between movement amplitude and cue type. Second, we will randomly introduce an "abort signal", consisting of a small positional deflection of the control handle, to determine if pre-planned wrist movements can be aborted given the presentation of additional sensory information. This will be done to determine when in the movement initiation and execution cycle the movements are committed and unalterable and whether there is any difference in this timing as a function of the type of go-cue (visual only or visual plus vibration) used.

List of Written Publications

R. J. Nelson, C. A. McCandlish and V. D. Douglas. Reaction times differ for hand movements in response to visual vs. vibratory cues. *Somatosensory and Motor Research* 7(3) (In Press).

R. J. Nelson, B. N. Smith and V. D. Douglas. Relationships between sensory responsiveness and premovement activity in areas 3b and 1 of monkey primary somatosensory cortex. (Submitted *Exp Brain Res.*).

R. J. Nelson, B. Li, and V. D. Douglas. Sensory response enhancement and suppression of monkey primary somatosensory cortical neurons. (Submitted *Brain Res. Bull.*)

Presentations of Supported Work

R. J. Nelson and V. D. Douglas. Differences in sensorimotor integration in cortical areas 3b and 1 of the monkey. *Neuroscience Abst.* 15:659, 1989.

V. D. Douglas, C. A. McCandlish and **R. J. Nelson.** Reaction times differ when humans and monkeys make hand movements in response to visual as compared to vibratory cues. *Neuroscience Abst.* 15:729, 1989.

Submitted Abstracts

R. J. Nelson and V. D. Douglas. Responsiveness of primary somatosensory cortical neurons to vibratory stimuli during movement vs. no-movement tasks. *Neuroscience Abst.*(Submitted).

Associated Personnel

Vickie Douglas continues to be employed as a Research Assistant. She has, over the past several years, proved to be of crucial importance in the studies conducted under this grant. Her expertise in data analysis and behavioral training of monkeys is truly unique. She has also distinguished herself by presenting a portion of our work during last year's annual meeting of the Society for Neuroscience.

Interactions

1989 Society for Neuroscience Annual Meeting, Phoenix, AZ Oct. 29 - Nov. 3.
1990 Winter Conference on Brain Research, Snowmass, CO Jan. 27-Feb. 3.

New Discoveries

None.